

BLECHNUM SPICANT: HABITAT AND VIGOR OF OPTIMAL, MARGINAL, AND DISJUNCT POPULATIONS, AND FIELD OBSERVATIONS OF GAMETOPHYTES¹

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Species composition and abundance values for vascular plants were determined for four forest stands at Olympic Peninsula, Washington, and a stand in northern Idaho where the homosporous fern *Blechnum spicant* occurred. Vegetative vigor and reproductive vitality for *B. spicant* were estimated. Sterile frond length ranged from 47.9 cm at Twanoh to 19.0 cm at the Hoh Stand. Spore germination approached zero in the Hoh and Mason Mountain populations. The optimum habitat for *B. spicant*, represented by the Twanoh Stand, was wetter than mean sites in the *Tsuga heterophylla* zone, where *Oplopanax horridum* and *Lysichiton americanum* were abundant, *Oxalis oregana* was absent, and *Polystichum munitum* was uncommon. Species composition, density, and phenology were determined for mixed fern gametophyte populations at Lake Quinault. Gametophytes were first found in early fall, grew vigorously over the winter, and produced sporophytes through late spring. Female, bisexual, and male gametophytes occurred in mixed-species populations at densities up to 4.5 cm⁻². Sporophytes appeared shortly after development of archegonia on bisexual and female gametophytes. Polyembryony did not occur. As almost all archegoniate plants bore sporophytes in dense populations, competition among gametophytes was thought to be minimal. Dense populations of young sporophytes later occupied sites sufficient for single perennating sporophytes. I hypothesized that strong competition occurs between young sporophytes and that gametophyte reproductive mechanisms that increase heterozygosity will be selected in dense populations.

Introduction

Blechnum spicant (L.) J. Sm. is unique in that it is a circumboreal fern in an otherwise tropical family of 200 species (COPELAND 1947). Fern sporophytes are typically noted in plant community studies (WARING and MAJOR 1964; DAUBENMIRE and DAUBENMIRE 1968), but with a few exceptions, their autecology has received little emphasis (PERRING and GARDINER 1976; NOBEL 1978). Characterization of fern habitats has been based on the conspicuous sporophyte generation, but it is possible that the inconspicuous gametophyte has made comparable adaptations and that measures of the variation of both generations would contribute to an understanding of adaptation (GILBERT 1970; FARRAR and GOOCH 1975; SCHNELLER 1975; TRYON and VITALE 1977; COUSENS 1979).

This study characterized vascular plant species composition and abundance in five plant communities in which *B. spicant* ranged from being rare to common. Vegetative vigor and reproductive vitality were assessed for *B. spicant* in these five communities. Naturally occurring gametophyte populations, which included *B. spicant*, were studied at the stand determined to be modal for the species.

Material and methods

Overstory vegetation was analyzed for a 15 × 25-m plot located in a homogeneous forest (DAUBENMIRE 1968). All trees taller than 50 cm were tallied by diameter class, and seedlings less than 50 cm tall were counted in two 1 × 25-m nested subplots.

¹ An appendix of species values and absolute values for vigor and vitality data is available from the author.

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Canopy coverage and frequency were estimated for 75 20 × 50-cm microplots placed at 1-m intervals along three 25-m transects in the larger plot (DAUBENMIRE 1959). Coverage was estimated by referring to the six coverage classes of DAUBENMIRE; frequency is the percentage of microplots in which a species occurs.

Vegetative vigor of *Blechnum spicant* was estimated by measuring the length and width of sterile fronds that represented 50 of the largest (oldest) plants in the center of each stand and by counting their fertile fronds. An estimate of the population structure of *B. spicant* was made at Lake Quinault by tallying all *B. spicant* plants found in three 15-m transects sampled with a 20 × 50-cm frame placed at 1-m intervals. Plants were placed in one of six life-history classes: (1) gametophytes; (2) gametophytes with sporophytes; (3) sporophytes, all juvenile leaves; (4) sporophytes, mixed juvenile and adult leaves; (5) sporophytes, all adult leaves, sterile; and (6) sporophytes, all adult leaves, including fertile.

Spore production by individual plants was determined by the volume displaced by spores in standard collection vials. Length and width of 20 randomly selected spores for each of 9-21 plants from each stand were determined. Germination was tested on approximately 300 spores on agar-solidified mineral medium (COUSENS 1979), kept for 14 h daily under 2,700-4,400 lx of fluorescent and incandescent light. After 15 days, germination was determined for 100 spores, as indicated by swelling and greening of the protoplast and emergence of a rhizoid. Spore viability following storage at 20 C was determined by testing germination at intervals up to 14 mo.

Naturally occurring populations of fern gametophytes were found at the Lake Quinault stand in

September 1970, January and June 1971, and August 1975. In addition to extensive populations of gametophytes on soil slips, small populations and isolated gametophytes were found by an intensive search within a 20 × 50-cm frame placed at 1-m intervals along a 15-m transect. Population density, gametophytes cm⁻², was determined by outlining gametophytes on acetate sheets laid over the plants and distinguishing those with sporophytes. Many small gametophytes that were not evident in the field could be counted on soil samples brought into the laboratory and examined with a dissecting microscope. Gametophytes were cleaned and fixed in warm acetocarmine and mounted in Hoyer's medium (BEEKS 1955). Identification of 95% of the collections was made by constructing a key based on morphological characters. *Blechnum spicant* gametophytes were characterized by fewer than six 8–12-μm trichomes that lack the waxy cap of the aspidioid ferns (COUSENS and HORNER 1970) and by an elongated basal cell supporting the antheridium (STOKEY and ATKINSON 1952). Some *B. spicant* gametophytes might have been passed over due to lack of these characters, but none would be misidentified as *B. spicant*. Sex expression, width, and developmental stage in *B. spicant* gametophytes were recorded. Growth rate was estimated by comparison with laboratory cultures (COUSENS 1979).

Vouchers for populations of *Blechnum spicant* were deposited in the herbarium at the University of Oregon Natural History Museum, Eugene (ORE). Vouchers for other vascular plants were deposited at the Marian Ownbey Herbarium, Washington State University, Pullman (WS). Nomenclature follows HITCHCOCK et al. (1955–1969).

Results

Specific location, climatic data, and notes for the Lake Quinault (LQ), Hoh River Valley (H), Mason Mountain (MM), Twanoh State Park (T), and North Fork (NF) stands are summarized in table 1. At the first four stands, continuous populations of *Blechnum spicant* on the Olympic Peninsula were sampled. At NF, a small population of *B. spicant* in Idaho 560 km disjunct from the nearest Olympic Peninsula stand was sampled.

Tsuga heterophylla is represented by an unbroken size-class distribution at all Olympic Peninsula stands and is replacing itself (table 2). The broken size-class distributions of *Picea sitchensis* and *Pseudotsuga menziesii* at LQ suggest that this stand closely approximates climax forest for the region. The LQ stand was characterized by 25% summed shrub coverage (table 3) including three conspicuous *Rubus* species poorly represented at H and absent from MM. *Polystichum munitum*, *Oxalis oregana*, and

TABLE 1
LOCATIONS OF THE STANDS AND CLIMATIC DATA

Stand name and location	Elevation (m)	Mean January/July temperature (°C)	Annual precipitation (cm)	Annual snowfall (cm)	Notes
Lake Quinault (LQ): Grays Harbor County, Wash.; T N23, R 9W, Sect 19....	80	3.9/17.2	340	20.5	Continuous distribution of <i>Blechnum spicant</i> . In near climax <i>Tsuga heterophylla</i> forest. In fog belt.
Hoh River Valley (H): Jefferson County, Wash.; T N27, R 10W, Sect 16....	125	...	320	11.7	Continuous distribution of <i>B. spicant</i> . Second terrace of Hoh River—available for colonization for 750 yr (FONDA 1974). In fog belt.
Mason Mountain (MM): Mason County, Wash.; T N24 R 4W, Sect 24....	990	2.8/18.3	254	66.9	Continuous distribution of <i>B. spicant</i> . Eastern edge of Olympic Mountains where slopes fall steeply to Hood Canal. In Rain-shadow, above fog belt.
Twanoh State Park (T): Mason County, Wash.; T N22, R 2W, Sect 30....	15	2.8/18.3	254	66.9	Continuous distribution of <i>B. spicant</i> . Poorly drained low coastal plain soil of glacial origin, topography of small hummocks and wet depressions.
North Fork (NF): Clearwater County, Idaho; T N40, R 10E, Sect 32....	960	-4.3/18.3	104	270.0	Disjunct population of <i>B. spicant</i> . Population limited to 200 × 500-m area on 35% slope 560 km from nearest Olympic Peninsula population.

NOTE.—Washington climatic data are from Quinault Ranger Station (LQ), Spruce Ranger Station (H), and Cushman Dam, which is equidistant between MM and T (PHILLIPS 1965). Idaho climatic data are from Pierce Ranger Station, which is 65 km from NF (RICE 1971). T = township, R = range, Sect = section.

TABLE 2
OVERSTORY COMPOSITION AND DIAMETER FOR THE FIVE STUDY SITES

SITE AND SPECIES	CLASSES OF dbh (dm)										
	0-1		1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10
	<.5 m	>.5 m									
Lake Quinault:											
<i>Tsuga heterophylla</i>	36	19	5	6	2		1		1		1
<i>Acer circinatum</i>	21	2									
<i>Thuja plicata</i>	1										
<i>Pseudotsuga menziesii</i>											6
<i>Picea sitchensis</i>							1		1		
<i>Alnus rubra</i>	1										
<i>Cornus nuttallii</i>	1										
Hoh River Valley:											
<i>T. heterophylla</i>	299		1	1	3		1		2		
<i>A. circinatum</i>	1	7	6	1							
<i>P. menziesii</i>											4
<i>P. sitchensis</i>	282					2			1		3
Mason Mountain:											
<i>T. plicata</i>	23	31		1		1	1	1			
<i>T. heterophylla</i>	19					1	1	2			
<i>P. menziesii</i>				1			5	1	1		
<i>A. circinatum</i>		1									
Twanoh State Park:											
<i>T. heterophylla</i>	80	8	2		4	1	1	2		1	2
<i>T. plicata</i>	40	2				1					4
<i>Acer macrophyllum</i>		2						1			
<i>Alnus rubra</i>		3					1				
<i>Fraxinus</i> sp.....		1									
<i>Rhamnus purshiana</i>		1									
North Fork:											
<i>T. plicata</i>	233		2	2	2	3	1				
<i>Abies grandis</i>	81	21						1			
<i>Pinus monticola</i>	2	1									
<i>Tsuga mertensiana</i>											(1)*

* Adjacent to but not encountered in sample.

TABLE 3
SUMMED COVERAGES OF UNDERSTORY PLANT GROUPS AT FIVE SITES

Plant group	LQ	H	MM	T	NF
Forbs.....	48	50	5	28	41
Shrubs.....	25	6	77	51	23
Pteridophytes.....	37	35	12	62	15
Species coverage/frequency:					
<i>Adiantum pedatum</i>	a	1/1	1/6
<i>Athyrium filix-femina</i>	2/28	1/12	1/5	11/40	10/21
<i>Blechnum spicant</i>	4/38	1/12	2/8	41/68	3/16
<i>Dryopteris arguta</i>	a
<i>D. carthusiana</i>	a
<i>D. dilatata</i>	a	a
<i>Equisetum telmateia</i>	a	1/14	...
<i>Gymnocarpium dryopteris</i>	1/4	1/1	...	2/6	...
<i>Lycopodium clavatum</i>	a
<i>Polypodium glycyrrhiza</i>	a
<i>P. hesperium</i>	a
<i>Polystichum munium</i>	29/53	32/50	9/36	5/16	1/4
<i>Pteridium aquilinum</i>	1/1	1/2	...
<i>Selaginella oregana</i>	a
Graminoids.....	1	6	0	5	7
Bryophytes.....	51	42	52	24	24
No. of vascular species.....	31	19	17	37	46

* Adjacent to but not encountered in sample.

Tiarella trifoliata var. *trifoliata* were the most abundant herbaceous plants at LQ and H. The overstory sample at LQ is similar to the "*Tsuga heterophylla*-*Thuja plicata* valley wall forest" (FONDA 1974), and abundant understory plants are those that characterize modal moisture stress sites in *T. heterophylla* forests (FRANKLIN and DYRNESS 1973).

Picea sitchensis is represented by a complete size-class distribution at H, suggesting that this stand represents an earlier successional stage than LQ. Forest composition is similar to FONDA's (1974) characterization of the second terrace of the Hoh River. Although species composition at H is similar to LQ, the reduced abundance of epiphytic mosses and pteridophytes (*Selaginella oregana*, *Polypodium glycyrrhiza*), reduced shrub coverage, and absence of *T. plicata* differentiate it from LQ (tables 2, 3). During August of 1970 and 1971 the soil surface at H was dry, but it remained moist at LQ.

The size-class distribution of *P. menziesii* at MM (table 2) indicates an earlier successional stage than either LQ or H and may reflect response to a major fire 300 yr ago (FONDA 1974). The MM and T stands are beyond the distribution of the coastal *P. sitchensis*. Shrub coverage at MM was the highest of all stands at 77%; *Gaultheria shallon*, *Rhododendron macrophyllum*, *Vaccinium membranaceum*, and *Berberis nervosa* were dominant in this layer. *Polystichum munitum* was the only herbaceous plant with coverage greater than 2%; *O. oregana* and *T. trifoliata* were absent. The absence of *O. oregana* and *T. trifoliata* and the dominance of ericaceous shrubs indicate xeric habitats within the *T. heterophylla* zone (FRANKLIN and DYRNESS 1973).

The presence of *Acer macrophyllum* and *Alnus rubra* in addition to *Tsuga* and *Thuja* is consistent with the poor drainage of the T stand (table 2). Shrub coverage totaled 51% with *Oplopanax horridum*, absent from all other stands, most conspicuous (table 3). *Blechnum spicant*, *Athyrium filix-femina*, and *Lysichitum americanum* were the most abundant herbaceous plants at T. *Oxalis oregana* was absent, and *P. munitum* coverage was relatively low.

The NF stand had the highest species number of all stands, and half of these were shared by at least one Olympic Peninsula stand. *Thuja plicata* appears to be the dominant tree; the stand is additionally characterized by *Abies grandis* and *Pinus monticola*. All three tree species are replacing themselves (table 2). *Linnaea borealis* and *Cornus canadensis* contributed half of the 23% shrub coverage; *A. filix-femina* and *Boykinia major* were the most conspicuous herbaceous plants. Except for the unusual occurrence of *B. spicant*, the vegetation of the NF stand was essentially that of the *T. plicata*-*A. filix-femina* habitat type (DAUBENMIRE and DAUBENMIRE 1968).

Summed pteridophyte coverage was moderate and equal at LQ and H, substantially lower at the MM and NF stands, and highest at T (table 3). Coverage and frequency values for *B. spicant* indicate the range of its success in the five stands (table 3, fig. 1). Values at LQ represent the abundance of this fern throughout the *T. heterophylla* forest of the western Olympic Peninsula. Lower values at H reflect reduced size of individual plants and relative rarity.

The life-history class distribution of *B. spicant* at LQ is bimodal with gametophytes most numerous (table 4). Nearly equal numbers of sterile and fertile adult plants suggest that a plant may remain sterile for several years before producing fertile fronds.

Sterile frond size (fig. 1) was greatest at the T stand and reached less than half of the T value at the H stand. Sterile frond size was intermediate at the remaining three stands and was similar to the species mean (FRYE 1934). The H plants produced only a single fertile frond, and T plants produced nearly twice that produced by the remaining three populations (fig. 1).

Spore production by *B. spicant* individuals ranged from 0.1 cm³ at H to 0.84 cm³ at T. Greater spore production typically correlated with greater fertile frond number, but MM plants with fewer and smaller fertile fronds yielded more spores than LQ plants (fig. 1). Some individual sporophytes in the H population yielded fewer than 300 spores from a single fertile frond. Spore size did not differ substantially among the populations, and morphologically abnormal spores were less than 2% in all populations.

Mean spore germination was highest immediately after collection (fig. 1). Initial germination values were similarly high for LQ, T, and NF populations and were very low for H and MM (fig. 1). Only seven of 21 H plants provided viable spores, and the highest single value for initial germination was 11%. Spore viability decreased to almost zero for H and MM collections after 2 mo, whereas substantial viability was demonstrated for other populations following 14 mo of storage.

Gametophyte populations were discovered in three ways: Populations that colonized large areas

TABLE 4
BLECHNUM SPICANT LIFE-HISTORY CLASS
DISTRIBUTION AT LQ

Class	No.
1. Gametophyte.....	260
2. Gametophyte with attached sporophyte.....	16
3. Sporophyte, all juvenile leaves.....	7
4. Sporophyte, mixed juvenile and adult leaves....	8
5. Sporophyte, all adult leaves, sterile.....	21
6. Sporophyte, all adult leaves, some fertile.....	20

NOTE.—Summed sample for 45 20 × 50-cm samples at 1-m intervals for three 15-m transects.

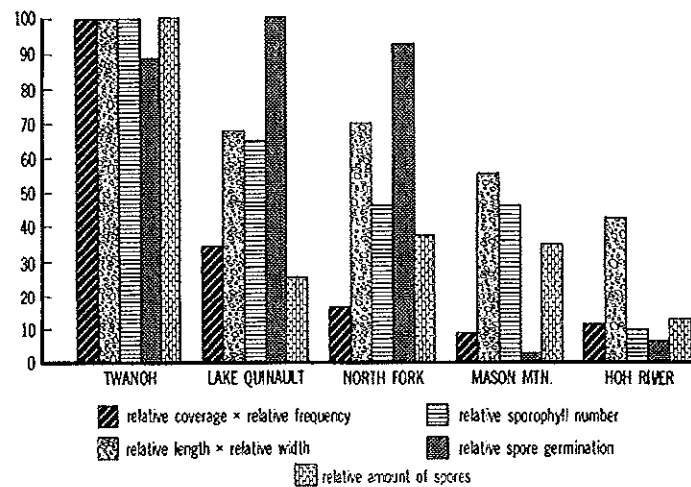
Relative Vigor and Vitality of *Blechnum Spicant* at Five Study Sites

FIG. 1.—Actual maximum values for coverage, frequency, frond length and width, sporophyll number, spore germination, and volume of spores produced are set to equal 100%. All other values are expressed relative to this maximum. Relative abundance of *Blechnum spicant* is expressed as relative coverage × relative frequency. Relative frond size is expressed as relative length × relative width. Study sites are arranged, left to right, in order of maximum to minimum total values for vigor and vitality of *B. spicant*.

of soil where a cover of mosses and *Selaginella oregana* had slipped were easily found ("soil-slip" populations); smaller populations were often found on clods of soil ("soil clods") turned up by elk and deer; and isolated gametophytes ("isolates") were found only by systematic sampling of undisturbed forest floor (table 5).

With the exception of *P. glycyrrhiza*, which produces spores in early spring, all ferns whose gametophytes were identified in natural populations at LQ shed their spores from mid-July through October. Mixed-species populations of gametophytes were first found in late summer, continued to grow through the winter, and were collected as late as June of the following year.

Species composition of the gametophyte populations (table 5) showed that *P. munitum* gametophytes were less abundant than their sporophytes

in all three types of samples (table 3). *Adiantum pedatum* sporophytes were limited to creek walls and especially moist sites and were not encountered in the understory samples on uplands (table 3); yet *Adiantum* gametophytes were quite common on the soil-slip population in the upland stand observed from 1970 to 1971, and even more abundant on soil clods in the same well-drained area (table 5). A soil-slip population adjacent to a creek wall stand of *A. pedatum* sporophytes was dominated by *A. pedatum* gametophytes (table 5). *Athyrium filix-femina* sporophytes were less abundant than *P. munitum* and *B. spicant*, but its gametophytes were common in all three types of populations (table 5).

Gametophyte population density for a soil slip observed repeatedly from 1970 to 1971, and for the soil-slip population adjacent to an *A. pedatum* sporophyte population observed in 1975, showed

TABLE 5
PERCENTAGE OF SPECIES COMPOSITION OF MIXED GAMETOPHYTE POPULATIONS AT LQ

	Total gametophytes	<i>Blechnum spicant</i>	<i>Polystichum munitum</i>	<i>Athyrium filix-femina</i>	<i>Adiantum pedatum</i>	<i>Polypodium glycyrrhiza</i>	Unidentified
Soil-slip populations:							
Continuous observations:							
9/10/70.....	215	24	8	30	26	4	8
1/27/71.....	149	34	5	31	28	0	2
6/6/71.....	100	39	6	19	28	2	6
Single observation:							
8/10/75.....	650	6	19	13	47	0	15
Soil clods:							
9/10/70.....	52	6	2	45	45	0	2
9/10/70.....	53	4	0	41	49	2	4
Isolates:							
6/6/71.....	6	33	0	33	33	0	0

maximum density in August 1975 (table 6). Density of the soil-slip population decreased from 3.5 cm⁻² to 1.9 cm⁻² over the winter of 1970-1971 as the area was eroded by rain.

Sex expression, presence of sporophytes, and width for gametophytes identified as *B. spicant* in the mixed populations show that presexual, bisexual, female, and male gametophytes were found in all soil-slip populations where density was high (table 7). Although population density on soil clods was comparable to that of soil-slip populations, a lower proportion of these gametophytes was determined to be *B. spicant* (table 5), and these were either female or male (table 7). Two isolated gametophytes identified as *B. spicant* were bisexual.

A low percentage of new sporophytes was found among soil-slip populations as early as September 1970 and August 1975. By January 1970, two-thirds of the gametophytes that bore archegonia produced sporophytes. This proportion was reduced in June by the addition of young plants to the population (table 7). It is difficult to distinguish between sporophyte-bearing bisexual and female gametophytes since antheridia typically occur at the base of the plant, an area which is often necrotic by the time a visible sporophyte is produced. Among the

B. spicant gametophytes found in soil-slip populations in January that bore embryos or older sporophytes, eight had intact bases. Two of these were female and six were bisexual.

Blechnum spicant gametophytes increased in width from September to January, and mean widths for each sex-expression type were smaller in June, suggesting that new plants were added to the population during winter. Female gametophytes were widest in all samples, bisexual plants were somewhat smaller, and male plants were approximately half the width of bisexual plants (table 7).

Discussion

Blechnum spicant completes its life cycle and is a regular member of the widespread plant community represented by the LQ stand. Habitats similar to the LQ stand occupy large areas on the Olympic Peninsula, and it appears that most *B. spicant* individuals occur in this suboptimal habitat. *Blechnum spicant* responds vigorously to increased moisture, as evidenced by its increased abundance and size in steep depressions that dissect the dome-shaped upland of the LQ stand. *Oplopanax horridum* also increases in these microhabitats while *Polystichum munitum* decreases.

The life requirements of *B. spicant* were not well met at the H stand, where the plants are dwarfed and produce few sporophylls. Minimal spore germination values suggest that edaphic characteristics of the second terrace of the Hoh River, which are ameliorated by succession to upland forest, limit the success of this plant. Adjacent upland stands at H support *B. spicant* sporophytes comparable in abundance and size to those at LQ, and it is possible that these more vigorous plants shower spores on the second terrace to maintain a sporophyte population.

TABLE 6

POPULATION DENSITY OF GAMETOPHYTES ON
LARGE SOIL SLIPS AT LQ

Collection date	Density	Density range	Mean width
September 10, 1970.	3.5 cm ⁻²	1-40	.9 mm
January 27, 1971...	2.8 cm ⁻²	0-27	2.5 mm
June 6, 1971.....	1.9 cm ⁻²	0-12	2.3 mm
August 10, 1975....	4.5 cm ⁻²	0-20	1.7 mm

TABLE 7

SEX EXPRESSION, WIDTH, APPROXIMATE AGE, AND PERCENTAGE OF SPOROPHYTES OF *B. SPICANT*
GAMETOPHYTES IN MIXED POPULATIONS

	PRESEXUAL			BISexual			FEMALE			MALE			WITH SPOROPHYTE (%)	TOTAL GAMETOPHYTE
	%	Size	Age ^a	%	Size	Age	%	Size	Age	%	Size	Age		
Soil-slip populations:														
Continuous observations:														
9/10/70.....	27	.4	17	8	2.0	40	5	1.8	32	60	.8	29	2	51
1/27/71.....	4	1.5	20	14	4.0	100	18	4.6	85	64	1.7	75	66 ^b	50
6/6/71.....	10	1.0	20	39	3.0	75	25	3.1	50	26	1.2	37	40 ^b	39
8/10/75 (washed out)														
Single observation:														
8/10/75.....	5	.3	15	17	2.1	50	34	2.9	50	44	.9	30	5	39
Soil clods:														
9/10/70.....	66	3.2	55	33	.8	29	0	3
9/10/70.....	100	3.5	90	0	3
Isolates:														
6/6/71.....	100	3.4	85	2

^a Age = age in days of lab-grown *B. spicant* gametophytes of comparable size.

^b Includes approximately 25% with sporophytes whose sex expression could not be determined due to necrotic bases.

Blechnum spicant appears to be at the xeric edge of its range of tolerance at the MM stand where June through August are relatively dry (PHILLIPS 1965). Although they are uncommon, individual *B. spicant* plants are not dwarfed, and sporophyll number and total spore production are greater than at H. However, spore germination approaches zero, and it appears that completion of the life cycle would be limited.

Production of spores with low germination at the H and MM stands may reflect limiting environmental factors during the year of their production. Cyclical years more favorable to spore production need occur only once during the lifespan of the perennial plant to allow persistence of the population.

Based on measures of abundance and indices of vigor and vitality, *B. spicant* is most successful in the poorly drained *Tsuga-Thuja* swamp at T where understory dominance is shared with *Oplopanax horridum*, *Athyrium filix-femina*, and *Lysichitum americanum* (fig. 1). The optimum moisture balance for *Oxalis oregana* is apparently exceeded in such habitats, and *Polystichum munitum*, the most abundant fern on the Olympic Peninsula, has lower coverage and frequency values than *B. spicant* and *A. filix-femina* in the habitat. Similar habitats are found throughout lowlands of the Olympic Peninsula and along the West Coast down to northern California where *B. spicant* occurs with *Darlingtonia californica*.

The isolated population of *B. spicant* in Idaho is comparable in abundance, vigor, and vitality to mean values for Olympic Peninsula populations. Neither the values used to assess vigor and vitality nor morphological characters used to determine subspecies distinguished the Idaho plants from those on the Olympic Peninsula; yet the persistence of this plant where air temperatures are strikingly colder, growing season is shorter, and snowfall is more abundant and persistent suggests that physiological adaptations may have occurred to differentiate this population.

Based on the occurrence of *B. spicant*, one would postulate that the NF site is warmer than the mean for the area, but the surprising occurrence of a few individuals of *Tsuga mertensiana*, mountain hemlock, succeeding at a substantially lower elevation than is characteristic, confounds such a simple hypothesis.

The gametophyte populations at LQ demonstrate that fern gametophytes may be found in mixed-species colonies, and where pteridophyte diversity of the stand is relatively low, these can be identified by morphological characteristics. For each species, relative abundance of gametophytes does not parallel that of sporophytes. Density of natural gametophyte populations varies from isolates to numbers comparable to those responsible for in-

creased antheridia production in culture (COUSENS and HORNER 1970).

The failure of dense soil-slip populations to establish mature sporophytes suggests that isolated gametophytes, and smaller colonies situated less precariously, may be more likely to complete the life cycle. Although the search for such plants requires more effort and does not uncover substantial numbers, such an emphasis may distinguish those gametophytes that are important to continuation of the species from those that function as ephemeral bryophyte-like plants in binding the soil and allowing replacement by other organisms.

If dense soil-slip populations contribute mature sporophytes to the community, it seems likely that strong selection will occur among the very young sporophytes. This is similar to competition among seedlings of many forest trees (HETT and LOUKS 1971). The discovery by FARRAR and GOOCH (1975) of a large population of young sporophytes, apparently arrested in growth, is consistent with this hypothesis.

Blechnum spicant gametophyte samples consisted of male, bisexual, and female plants, and the proportion of these types shifted during the fall to late spring growing season. In both the field collections reported here and in laboratory cultures (COUSENS 1979), female gametophytes were largest, bisexual plants somewhat smaller, and male plants smallest. This is consistent with NÄR's (1956) conclusion that antheridogen production diverts potential vegetative growth. Variable sex expression resulted in intergametophytic mating as evidenced by the discovery of female gametophytes that bore sporophytes in soil-slip populations, and intragametophytic selfing was demonstrated by the appearance of sporophytes on isolated bisexual gametophytes of *B. spicant*. It is possible that such variation is mediated by an antheridogen (TRYON and VITALE 1977; COUSENS 1979).

The decrease in the proportion of male gametophytes of *B. spicant* from January to June, and the increase in bisexual gametophytes over this interval, suggest that a good number of *B. spicant* gametophytes attain bisexuality following a prolonged male phase. Laboratory studies of sex expression for this population suggest that both male and female gametophytes may become bisexual (COUSENS 1979). It is difficult to quantify shifting patterns of sex expression in nature since new gametophytes may be added to the populations through prolonged spore release and delayed germination. A disproportionate number of male gametophytes may be lost to erosion since these smaller plants never have a rooted sporophyte to help anchor them.

Further variability in the phenology of natural populations of gametophytes is suggested by the observation that *B. spicant* gametophytes collected

in August 1975 were larger than those collected in September 1970 and had a higher proportion of sexual plants. A final difference between field collections of *B. spicant* gametophytes and those grown in chambers is that apparent growth rate of plants in nature is approximately half that in culture. This suggests a need for caution in extrapolating data from the laboratory and the need for continued field studies to test hypotheses suggested by laboratory studies.

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